

THE ORIGIN OF SLAVERY AMONG ANTS

By WILLIAM MORTON WHEELER

[Reprinted from THE POPULAR SCIENCE MONTHLY, Vol. LXXI., December, 1907]

THE ORIGIN OF SLAVERY AMONG ANTS

DR. WILLIAM MORTON WHEELER

AMERICAN MUSEUM OF NATURAL HISTORY

THE researches of the past few years have materially changed our views on the significance and phylogenetic origin of the so-called slave-making instincts among ants. And although the subject still involves many unsolved problems, we are now in a position to look back on its history and marvel at our too implicit confidence in certain analogies, at our neglect of the basic principles of phylogenetics, and at the inept questions we so long persisted in asking.

Slavery, or dulosis, is a rare phenomenon among ants. In its pure form it is known to occur only in two of the several thousand described species, namely, in the sanguinary or blood-red slave-maker (*Formica sanguinea*) and the amazon (*Polyergus rufescens*). These species, with their various subspecies and varieties, are peculiar to the north temperate portions of Europe, Asia and America. The phenomenon was first discovered by J. Pierre Huber (1810)¹ and most completely described by him and by Forel (1874)². These investigators, of course, fixed their attention on the behavior of the workers. To this aspect of the subject later writers have added little of importance, and have merely fallen into a natural error of continuing in the same path as their illustrious predecessors. This was the case, for example, with Darwin³ and with Wasmann, who for the past quarter of a century has been observing the slave-making ants of Europe. Huber and Forel showed that the workers of *F. sanguinea* and *P. rufescens* make periodical forays on colonies of ants belonging to the *F. fusca* group, carry home the worker cocoons and larvæ, and permit some of these to hatch and to survive with them in the same formicary. An eminently predatory species thus comes to live in intimate symbiosis with workers of an alien species which are said to function as slaves, or auxiliaries. *F. sanguinea* is a powerful and very plastic species which continues to exercise all the fundamental ant instincts in the presence of its slaves. It can excavate galleries in the soil, obtain its own food and bring up its own young. *Polyergus*, however, is abjectly dependent on its auxiliaries. It is no longer able to excavate a nest, care for its own

¹"Recherches sur les mœurs des fourmis indigènes," Paris et Genève, 1810.

²"Les Fourmis de la Suisse," Zürich, 1874.

³"On the Origin of Species by Means of Natural Selection," third edition, London, John Murray, 1861, p. 244.

offspring, or even to take food, except from the tongues of the alien workers. It is therefore properly considered as representing a more advanced stage of parasitism than *sanguinea*. A few species belonging to the Myrmicine genera *Tomognathus* and *Strongylognathus* seem to possess analogous instincts, but too little is known of their habits to enable us to make very definite statements concerning them.

It was, of course, impossible to do more than speculate on the phylogeny of the slave-making instincts of *sanguinea* and *Polyergus* without a knowledge of the ontogenetic source and development of these instincts, and as these are social activities, that is, carried out simultaneously by a number of cooperating organisms, it was necessary to learn something about the origin and development of the ant colony as a unit. The bearing on the origin of slavery of the obvious and fundamental fact that there is a double ontogeny and phylogeny in social organisms, namely, one of the colony as well as one of the individual, has been appreciated only within the past few years and has completely changed the aspect of the subject.

In the great majority of ant species the colony arises and develops in the following manner: The single female, or queen, after mating during her marriage flight, descends to the earth, divests herself of her wings, digs a small cell in the soil, or enters some preformed cavity under a stone or in the tissues of a plant, lays a number of eggs, feeds the resulting larvæ with a salivary secretion, and guards and nurses them till they mature and constitute a brood of diminutive workers. These now proceed to enlarge the nest, to forage for food, both for themselves and their mother, and to care for the succeeding broods of young. The queen thenceforth gives herself up exclusively to feeding from the tongues of her offspring and to laying eggs. The colony grows apace, the workers increasing in number, size and polymorphism with successive broods. Eventually males and virgin queens are produced, though often only after the expiration of several years, when the colony may be said to have completed its ontogenetic development.

It will be seen from the foregoing description that the mother queen lapses from the position of an independent organism with remarkable initiative to that of a parasite dependent on her own offspring. The latter stage in her life is of much longer duration than the former. This singular ontogenetic change in the instincts of the queen should be noted, as it foreshadows an important phylogenetic development exhibiting two different modifications, one of which is excessive, the other defective, in comparison with the primitive and independent type of colony formation. The excessive, or redundant, type is known to occur only among the Attiine ants of tropical America. These raise fungi for food and are quite unable to subsist on any other substances. The queens are often very large, especially in the typical

genus *Atta*, and not only manage to bring to maturity a brood of workers, but at the same time, as von Ihering,⁴ Goeldi⁵ and Jacob Huber⁶ have shown, have energy to spare to devote to the cultivation of a fungus garden. With the appearance of the first brood of workers, however, these queens, like those of most ants, degenerate into parasites on their own progeny.

This dependent stage, which, as I have said, is of much greater duration than the independent stage in the long life of the queen, leads to a number of phylogenetic developments of the defective type. These developments first manifest themselves in the adoption of young queens by adult workers of their own species. A word of explanation will make this clear. In the colonies of many species of Formicidæ we find several queens—in fact, there are comparatively few ants whose adult colonies do not contain more than one of these fertile individuals. And a study of the growth of such colonies shows that the supernumerary queens are either daughters of the original single queen that founded the colony, or have been adopted from other colonies of the same species. Hence these queens are either virgins, or have been impregnated by their own brothers (adelphogamy of Forel) in the parental nest, or have been captured by the workers and carried into the nest after descending from their nuptial flight. This forcible adoption leads necessarily to a complete suppression of the independent stage in the life of such queens. I have shown, in another article, that merely removing a queen ant's wings with tweezers will at once call forth the dependent series of instincts, and the same result is undoubtedly produced when the workers deilate the virgin or just-fertilized queens of their own or other formicaries. Such queens, finding themselves surrounded by a number of accomplished nurses, the workers, proceed at once to act like old queens that have already established their colonies and brought up a brood.

From this condition of facultative adoption to an obligatory adoption of the queen by workers of her own species is but a step. And here there are three possibilities: first, the queen can establish a colony only with the aid of workers of her own species and of the same colony. This condition seems not to obtain among ants, although it is well known in the honey-bees. Second, the queen must either be adopted by the workers of her own species of the same or another colony, or

⁴ "Die Anlage neuer Kolonien und Pilzgärten bei *Atta sexdens*," *Zool. Anz.*, XXI., 1898, pp. 238-245, 1 fig.

⁵ "Beobachtungen über die erste Anlage einer neuen Kolonie von *Atta cephalotes*," *C. R. 6me Congr. Internat. Zool.*, Berne, 1905, pp. 457-458, and "Myrmecologische Mitteilung das Wachsen des Pilzgartens bei *Atta cephalotes* betreffend," *ibid.*, pp. 508-509.

⁶ "Ueber die Kolonienegründung bei *Atta sexdens*," *Biol. Centralbl.*, XXV., 1905, pp. 606-619, 625-635, 26 figs.

by workers of an alien species. This is the case with many queen ants that have lost the power of establishing colonies unaided. Third, the queen must always be adopted by an alien species. This is the case in certain ants, especially in the highly parasitic forms that have lost their worker caste. The three conditions here enumerated clearly represent the transition from parasitism of the queen on the same, to parasitism on an alien species. The latter alone is commonly regarded as true parasitism, but the former, which, of course, can occur only among social organisms or during social stages in the lives of solitary organisms, is parasitism in every essential particular. It is not confined to ants and other social insects, but has analogies also in human societies (trusts, "grafters," criminal and ecclesiastical organizations) and in human families (when the parents become senile).

Ant colonies are such closed and exclusive societies that the adoption of strange queens, even of the same species but from alien colonies, usually meets with insuperable opposition on the part of the workers, and, as a rule, female ants have to overcome even greater hostility when they seek adoption in colonies of alien species. There are, nevertheless, at least three different methods of overcoming this hostility and of effecting an adoption. These may be taken to characterize three different forms of social parasitism, as follows:

1. *Temporary Social Parasitism*.—I have given this name to a form of parasitism which I first observed in our American *Formica difficilis* var. *consocians*.⁷ The fertilized female of this ant, quite unable to found a colony unaided, enters a colony of *F. schaufussi* var. *incerta* and is adopted with surprising facility. The queen of the latter species disappears, in some manner hitherto unknown, and the *consocians* brood is reared by the *incerta* workers, which, after functioning as nurses, gradually die off and leave a pure *consocians* colony thenceforth able to wax large and lead an independent and aggressive existence. This interesting type of parasitism occurs in most, if not all, *Formica* of the *exsecta* and *rufa* groups, both in America and in Europe, in a Myrmicine ant, *Aphenogaster tennesseensis* (parasitic on *A. fulva*) and in a Dolichoderine ant, *Bothriomyrmex meridionalis* (parasitic on *Tapinoma erraticum*). The females of these parasitic species tend to become greatly reduced in size (*F. difficilis* and several allied species: *F. dakotensis*, *microgyna*, *impeza*, *nepticula*, *suecica*, etc.) or at any rate to become smaller than the queens of their host species (*F. truncicola*, *wasmanni*, *oreas*, *ciliata*, *crinita*, *pressilabris*, etc.). This is clearly an adaptation to a mode of life for which an endowment of fat and vigorous muscle is not needed, since these various queens do not have to starve for weeks or even months while bringing up a brood

⁷ "A New Type of Social Parasitism Among Ants," *Bull. Am. Mus. Nat. Hist.*, XX., 1904, pp. 347-375.

of workers, as in the case of most ants. Santschi has recently made the illuminating discovery that the queen *Bothriomyrmex*, after entering the nest of *Tapinoma*, actually decapitates the queen of the host species and is adopted in her stead. In the other cases the disappearance of the host queen has not been accounted for. In the case of *F. incerta* it is conceivable that she may be ejected from the colony or be killed by her own workers as in the colonies of the Algerian *Monomorium salomonis* infested with *Wheeleriella*, a case to be considered presently. For the *consocians* type of social parasitism Santschi⁸ has suggested the name "tutelary" parasitism, because the young of this species are reared by workers older than the parasitic queen.

2. *Slavery, or Dulosis*.—In this case, as I have shown for the American *F. sanguinea*,⁹ the female enters a *Formica* colony belonging to some variety of the *F. fusca* or *schaufussi* group, kills or puts to flight the workers that attack her and hastily appropriates a number of worker larvæ or cocoons. These she carefully guards till they hatch, when she is surrounded by a loyal brood—of an alien species, to be sure, but nevertheless both able and inclined to bring up her brood when it appears. This is "pupillary" parasitism, to use Santschi's term, since the nurses, or host ants, are younger than the parasitic queen. In this case the queen of the host species is probably put to flight at the time the *sanguinea* queen enters the nest. *Polyergus rufescens* colonies are, perhaps, founded in the same manner, but unequivocal observations on the queens of this species are still lacking. Not only is slavery, at least as manifested in *sanguinea*, distinguished from the other forms of social parasitism by the aggressive behavior of the queen, but also by a peculiarity of her own workers. These inherit from their mother the instinct to enter nests of the host species, and appropriate the young, but these queen instincts are intimately associated with the feeding instincts of the workers, as the latter forage in companies like so many nondulotic ants and consume many of the captured pupæ. Hence the futility of all attempts, like those of Darwin and Wasmann, to understand slavery from a study of the behavior of the workers alone.

Wasmann¹⁰ and Santschi believe that slavery has arisen from temporary parasitism, but although I myself first advanced this opinion, I have been compelled to abandon it. Wasmann found that a colony of *Formica truncicola*, which he has shown to be a temporary social para-

⁸ "A Propos des Mœurs Parasitiques Temporaires des Fourmis du Genre *Bothriomyrmex*," *Ann. Soc. Entom. France*, 1906, pp. 363-392.

⁹ "On the Founding of Colonies by Queen Ants, with Special Reference to the Parasitic and Slave-making Species," *Bull. Am. Mus. Nat. Hist.*, XXII, 1906, pp. 33-105, pls. VIII.-XIV.

¹⁰ "Ursprung und Entwicklung der Sklaverei bei den Ameisen," *Biol. Centralbl.*, XXV., 1905, pp. 117-127, 129-144, 161-169, 193-216, 256-270, 273-292.

site in all essential respects like *F. consocians*, would accept and rear *fusca* pupæ placed in the nest. This, however, is not dulosis. In order to establish his case he would have to prove that the *truncicola* workers can also make periodical forays on *fusca* for the sake of capturing their young, and there is no more evidence that *truncicola* can do this than there is of similar behavior on the part of *consocians*. Santschi, if I understand him correctly, believes that the *sanguinea* colony restricts its forays to the scattered fragments of the original *fusca* colony from which the queen secured her first supply of auxiliaries, and that the slave-making expeditions cease when these fragments are exhausted. This assumption seems to explain the fact that old *sanguinea* colonies are sometimes slaveless and pure, like the adult colonies of *consocians*, *truncicola*, etc. It is, however, rendered highly improbable by the fact that both in Europe and in North America *sanguinea* colonies not infrequently contain slaves of two or more different species or varieties. There is also some evidence that the same colony may have slaves of different species at different times. Professor Forel recently showed me near Morges, Switzerland, a colony of *Polyergus* which in 1904 contained only *F. rufibarbis*, but during the current year contained only *F. glebaria*. The similarity between old *sanguinea* colonies and adult colonies of temporary parasites like *F. consocians*, is more probably the result of two very different processes: in the former case of a languishing or lapsing of the slave-making instincts with age, in the latter, as I have shown, of a gradual extinction of the tutelary workers.

3. *Permanent Social Parasitism*.—This occurs in the following rare and monotypic Myrmicine ants: the European *Anergates atratulus*, parasitic on *Tetramorium caespitum*, the Tunisian *Wheeleriella santschii*, parasitic on *Monomorium salomonis*, the North American *Epocus pergandei* (on *Monomorium minutum* var. *minimum*), *Sympheidole elecebra* (on *Pheidole ceres*) and *Epipheidole inquilina* (on *Ph. pilifera coloradensis*). All these parasites are unique among ants in lacking a worker caste, so that they are compelled to live permanently with their respective host species. Santschi¹¹ has recently shown that the just-fecundated queen of *Wheeleriella* enters a *Monomorium* colony and is adopted by the workers, which then actually proceed to kill their own queen. The same conditions probably obtain also in the other cases, as the parasitic queens are too feeble to assassinate the host queen after the manner of *Bothriomyrmex*. In *Anergates* the degeneration of the species as a result of permanent parasitism is extreme: the male is reduced to an apterous, pale and anæmic, sluggish, pupa-like creature which mates in the maternal nest with its own sisters (adelphogamy),

¹¹ Forel, "Meurs des Fourmis Parasites des Genres *Wheeleriella* et *Bothriomyrmex*," *Rev. Suisse Zool.*, XIV., 1906, pp. 51-69; "Nova Speco Kaj Nova Gentonomo de Formikoj," *Internacia Scienco Revuo*, 4° Jaro, 1907, pp. 144, 145.

as Forel has shown, and as I was able to observe during the past June in a large *Anergates-Tetramorium* colony at Vaux, Switzerland. This colony contained upwards of 1,000 winged female *Anergates* and several hundred males. Many of the former, placed on the craters of strange *Tetramorium* nests, entered these at once. The *Tetramorium* workers never killed these females, though they often seized them, carried them some distance from the nest and cast them away. The males, too, were not killed, although they were more forcibly and immediately ejected. This behavior is very suggestive, for *Tetramorium* workers when placed on the craters of strange colonies of their own species are at once pounced upon and killed.

It is not improbable that all three of these derivative types, namely, temporary, permanent and dulotic parasitism, have developed independently out of the primitive adoptive type of colony formation, although the details of this development are still very obscure. I have already given my reasons for believing that slavery did not arise directly from temporary parasitism. Owing to the excessive specialization of the permanent parasites and the loss of the worker caste among these species, it is not so easy to determine whether they have arisen from temporarily parasitic or from dulotic species, for it is conceivable that they may have arisen from either, especially as there are other ants, such as *Strongylognathus* and *Tomognathus*, which combine peculiarities of both of these categories. The species of *Strongylognathus* are peculiar to the palearctic fauna and, like *Anergates*, live with colonies of the extremely abundant and ubiquitous *Tetramorium caespitum*. The workers and females have sickle-shaped mandibles like *Polyergus*. Two species, *S. rehbinderi* and *S. huberi*, as Forel has shown, still possess vestiges of slave-making instincts. In *S. testaceus*, however, which is the common European form, the workers are greatly reduced in number, showing, as Forel has suggested, that this caste is on the eve of disappearing completely and thus leading to conditions like those of *Anergates* and the other permanent parasites. Wasmann once found a *S. testaceus-Tetramorium* colony containing fertile females of both species, and during the past June Professor Forel and I found a similar colony on the Petit Salève, near Geneva. This colony contained a fertile *Tetramorium* queen. The much smaller *Strongylognathus* queen could not be found, but must have been present, as there were young pupæ of this species in the nest. It is evident in this case, therefore, that the parasitic and host queens manage to live side by side (allometrobiosis of Forel). This condition arose, perhaps, from slavery or temporary parasitism by a suppression on the part of the *Strongylognathus* queen of the instinct to kill or drive away the *Tetramorium* queen.

The genus *Tomognathus* is represented in northern Europe by *T.*

sublavis (parasitic on *Leptothorax acervorum*) and in North America by *T. americanus* (parasitic on *L. curvispinosus*). The former was supposed by Adlerz¹² to have only ergatoid, or worker-like females, but Viehmeyer¹³ has recently found winged females as well, and I had previously shown that such individuals exist in our American form. The workers of both species resemble those of *Polyergus* and *Strongylognathus* in having blunted or obsolete domestic instincts. Adlerz's observations seem to indicate that the European *Tomognathus* may be dulotic, but they do not altogether preclude the possibility of permanent parasitism. As there are no observations on the behavior of the recently fecundated queens, it is impossible to decide whether the form of symbiosis exhibited by these ants arose from dulosis or from temporary parasitism or merely from a condition of xenobiosis like that of the North American *Leptothorax emersoni* or the European *Formicozenus nitidulus*.¹⁴

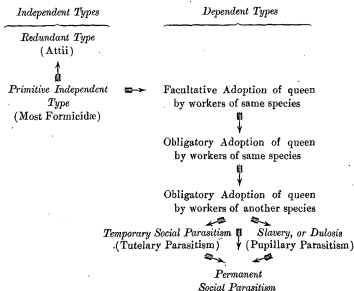
The accompanying diagram will serve to illustrate the phylogenetic relationships of the different types of colony formation among ants as formulated in the preceding paragraphs.

The foregoing discussion shows very clearly that a rational explanation of slavery among ants can be found only by recognizing the phenomenon as a form of parasitism. This conclusion is indeed forced upon us by a comparative study of the various allied forms of social symbiosis, of the ontogeny of the ant-colony, that is, of the way in which it is started and develops, and by a study of the instincts of the queen. We myrmecologists seem to have been hampered in reaching this conclusion by a knowledge of the habits of the queen honey-bee. This insect is peculiar in being permanently and exclusively in the adoptive

¹² "Myrmekologiska Studier—III, *Tomognathus sublavis* Mayr.," *Bih. Svensk. Vet. Akad. Handl.*, XXI, Afh. 4, 1896, 77 pp., 1 taf. .

¹³ "Beiträge zur Ameisenfauna des Königreiches Sachsen," *Abhandl. naturwiss. Gesell. Isis*, Dresden, 1906, Heft II., pp. 55-69, Taf. III.

¹⁴ Since the manuscript of this article was sent to press I have received from my friend, Mr. H. Viehmeyer, of Dresden, an interesting communication, in which he describes his experiments with a number of naturally dealated and therefore presumably fecundated queens of *Tomognathus sublavis*, *Formica sanguinea*, *Polyergus rufescens* and *F. truncicola*. These queens were introduced into strange colonies belonging to the normal hosts of their respective species. The results obtained with *F. sanguinea* and *truncicola* fully confirmed my observations on the American *sanguinea* and *consocians*. The queens of the typical European *Polyergus rufescens* were much more passive than those of the American subspecies *lucidus*, used in my experiments, and were adopted on the second or third day by the slave species *F. rufibarbis*, but not by *F. fusca* till a much longer period had elapsed. An ergatoid *Tomognathus* queen placed in a colony of *Leptothorax acervorum* "presented the same picture as *sanguinea*. The *Leptothorax* fled with their larvæ and then attacked the queen. During the course of the day, however, the latter managed to kill all of the *Leptothorax*."



or dependent stage, that is, she is unable to found a colony or even to exist apart from workers of her own species. And as the queen ant passes most of her life in similar dependence on her workers, namely, after establishing her colony, the earlier and more characteristic manifestations of her instincts and her marvelous initiative and plasticity were either disregarded or deemed to be of little importance. Attention was concentrated on the worker slave-makers whose activities represent a combination of queen and worker instincts. Darwin was thus led to derive the slave-making from the foraging instincts, and Wasmann—well Wasmann could only keep repeating or implying that the slave-making ants made slaves, because they were endowed with a slave-making instinct—a fine modern example of Molière's famous opium fallacy and of the resources of scholastic methods in zoology! Wasmann supposed that *F. sanguinea* is possessed of an extraordinary fondness for educating the young of the alien *fusca*. This was quite incomprehensible, especially as *sanguinea* workers are in no respect degenerate or dependent on their auxiliaries. Since I have examined many colonies of the European *sanguinea*, which, as a rule, rears much fewer auxiliaries than our American forms of the same species, Wasmann's assumption seems to me to be preposterous. After the habits of our temporary parasites and especially after the behavior of the young *sanguinea* queens had been studied, the relations of the dulotic species to particular hosts were easily understood, for the young queens are reared by workers of a particular host species (*fusca* or *schaufussi* or some of their varieties) or at any rate meet them frequently in the parental

nest. What is more natural, therefore, than that the queens, when ready to establish their colonies, should seek out the nests of these same species? The *sanguinea* workers, too, are reared by auxiliaries of the same species, so that we are not surprised to find that it is against colonies of these that the dulotic expeditions are directed. The absence of any tendency on the part of the *sanguinea* to rear or adopt the males and females of the host species may be due merely to a lack of familiarity of the slave-makers with these sexual forms, which in all probability are characterized by a peculiar odor unlike that of the co-specific workers.

Thus is dissipated much of the mystery with which the subject of slavery has been invested, and the phenomenon becomes intelligible as a form of parasitism in which the slaves are really the host. The dulotic ants differ from the temporary and permanent parasites not only in the peculiarity of the worker instincts, but also as representing parasites with a synthetic host. In other words, the workers, when they snatch the larvæ and pupæ from different nests of one or more varieties of *F. fusca* or *scharfussii*, are actually constructing a unitary colony out of fragments of several colonies of the host species. This peculiarity, as I have shown, arises from the inheritance of female instincts by the workers and a fusion of these with the foraging instincts which the worker slave-makers share with this caste in many other Formicidæ. Santschi expresses a similar opinion when he says: "In fine, slavery reduces itself to a form of pupillary parasitism that perpetuates and extends itself beyond the confines of the nest." His distinction of tutelary and pupillary parasitism is useful, as it calls attention to a more active and a more passive form of this phenomenon, but the distinction should not be overworked. Although the tutelary form would seem to lead more readily to permanent social parasitism with all its attendant degenerative characters, we must remember that *Polyergus*, though very passive in the hands of its slaves, is extremely aggressive when plundering the nests of the host species, whereas species like *F. consocians* and *truncicola*, though very passive in the earliest stages of colony formation, are very aggressive as soon as their colonies have emancipated themselves from the host species. The pupillary and tutelary types are, moreover, already foreshadowed as consecutive ontogenetic stages in the behavior of most ant-queens, for the independent stage in colony formation is pupillary, whereas the closing years of the queen's life are passed in a condition of tutelary parasitism on her own offspring and species.